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Spatiotemporal Variability in Coral (Anthozoa: Scleractinia) Larval Recruitment in the Southern Gulf of California¹

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Abstract: Sexual recruitment allows corals to maintain their populations through time, reach new habitats, and repopulate areas after an environmental or anthropogenic disturbance. This study aimed to estimate spatiotemporal variation of sexual recruitment along two areas of the southwestern coast of the Gulf of California (Bahía de La Paz and Bahía de Loreto) considered to be suboptimal for coral development (strong seasonality and variability of sea-surface temperature, incidence of hurricanes, turbidity and nutrient concentration, and low Ω_{ar}). Recruitment data were compared to sea-surface temperatures and with recruitment data from other sites in the eastern Pacific that have less-stressful environments. Terracotta tiles were used as collectors of larval coral propagules; tiles were immersed for 3-month periods between August 2004 and September 2005. Higher recruitment was found during the warm season, and coral recruits were found at almost all sites, including a vessel grounding area. Recruitment was higher in Bahía de La Paz $[12.80\pm29.57~\text{individuals}~\text{(ind)}~\text{m}^{-2}~\text{yr}^{-1}]$ than in Bahía de Loreto $(0.99 \pm 1.49 \text{ ind } \text{m}^{-2} \text{ yr}^{-1})$. Coral recruits belonged to five coral genera in Bahía de La Paz, with Porites as the dominant genus (102 recruits), followed by Pocillopora (six), Psammocora (three), Pavona, and Tubastraea (one each). At Bahía de Loreto, recruits of two coral genera were recorded: Porites (four) and Psammocora (one). Despite being conducted in a highly stressful environment, this study reports the second-highest rate of Porites recruits in the eastern Pacific and the first instance of *Psammocora* recruits (four ind) in the area.

Keywords: coral recruitment, restored reef, eastern Pacific, Mexican Pacific, artificial substrates settlement

HERMATYPIC CORAL populations are maintained by colony fragmentation and sexual larval recruitment (Smith and Hughes 1999, López-Pérez et al. 2007; Glynn, Colley, et al. 2017). During sexual recruitment, coral release propagules (i.e., gametes or larvae), which are scattered by water flow and settle near their origin area or reach new regions, promote genetic exchange and recolonize sites after natural or anthropogenic disturbances (Fox 2004, Miller and Ayre 2004, López-Pérez et al. 2007). Generally, the tim-

¹ Manuscript accepted 8 March 2018. This research was supported by funding from Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) grant CT001 to E.F.B.; R.A.C.-T. and D.A.P.-G. were recipients of a graduate fellowship from Consejo Nacional de Ciencia y Tecnología (CONACYT, No. 83339 and 160065).

Pacific Science (2018), vol. 72, no. 4:435–447 doi:10.2984/72.4.4 © 2018 by University of Hawai'i Press All rights reserved

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ing of coral sexual reproduction and recruitment depends on the environment, especially sea-surface temperature (SST), light, and nutrients, but other environmental conditions such as sedimentation, daily light/dark periods, and lunar cycles have also been related to coral reproduction in the eastern Pacific (Glynn, Colley, et al. 2017).

In recent years, sexual recruitment has been measured to understand how coral communities survive after natural or anthropogenic disturbances. However, most of these studies have been conducted in the Indo-Pacific and Caribbean regions (Babcock et al. 2003, Heyward and Negri 2010, Ritson-Williams et al. 2010). Sporadic studies have addressed coral sexual recruitment in the eastern Pacific. The first studies were carried out in Central America, where low recruitment rates were found [0 to 0.21 individuals (ind) m⁻² yr⁻¹ (Birkeland 1977, Wellington 1982, Richmond 1985)]. Studies done along the Pacific coast of Mexico showed higher recruitment rates [between 0.21 and 20.4 ind m⁻² yr⁻¹ (Reves-Bonilla and Calderon-Aguilera 1994, Glynn and Leyte-Morales 1997, Medina-Rosas et al. 2005, López-Pérez et al. 2007)]. Differences in recruitment rates between areas have been attributed to spatial and temporal variation in coral reproduction cycles and to different oceanographic conditions of each site and region (López-Pérez et al. 2007, Carpizo-Ituarte et al. 2011, Rodriguez-Troncoso et al. 2011, Chávez-Romo et al. 2013; Glynn, Colley, et al. 2017), especially to SST. Sexual reproduction studies conducted along the Pacific coast of Mexico on Pocillopora damicornis, Porites panamensis, and Pavona gigantea showed that egg development activity increases during periods of high SST (Chávez-Romo and Reves-Bonilla 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011); thus, larval recruit pulses are expected during warm seasons.

The Gulf of California is considered a stressful area for coral development, due to the large seasonal SST range, which is often associated with coral bleaching and mass mortality, high incidence of hurricanes, high turbidity and nutrient concentration due to upwelling events, naturally low pH and Ω_{ar} ,

and high pCO₂ (Reves-Bonilla et al. 2002, Manzello et al. 2008, Paz-García, Balart, and García-de-Léon 2012; Glynn, Alvarado, et al. 2017). Thus, sexual recruitment of corals in the area is expected to be low, because Glynn et al. (1991), Glynn et al. (1994), Glynn et al. (1996), Glynn et al. (2000), and Glynn et al. (2011) found that sexual reproduction in Central America is more common in environments that have optimal conditions through the year, and corals living in harsh environments often maintain their populations through asexual reproduction (fragmentation). Nevertheless, despite the stressful environmental conditions of the Gulf of California, histological (Chávez-Romo and Reyes-Bonilla 2007) and genetic studies (Aranceta-Garza et al. 2012; Paz-García, Chávez-Romo, et al. 2012; Pinzón et al. 2012; Chávez-Romo et al. 2013) indicate that sexual reproduction is frequent in the coral communities of the Gulf of California. However, no study has quantified coral larval recruitment in the area. To address this, our study describes the spatial-temporal variation of coral larval recruitment at 12 sites along the southwestern coast of the Gulf of California, including a restored reef affected by vessel grounding. Larval recruitment data were contrasted with SST of each studied area and with recruitment data from other sites in the Caribbean, Indo-Pacific, and eastern Pacific with more favorable environments for hermatypic coral development. Due to harsh environmental conditions, coral larval recruitment is expected to be low in our study areas (especially in Bahía de Loreto) in comparison with more environmentally favorable reef sites; recruitment pulses during the warm season are also expected because of dependency of coral reproduction cycles on SST.

MATERIALS AND METHODS

Study Sites

Coral recruitment was measured in two areas of the southern peninsular coast of the Gulf of California, Bahía de La Paz and Bahía de Loreto, where six sites were selected in each area. In Bahía de La Paz (Figure 1*a*), three

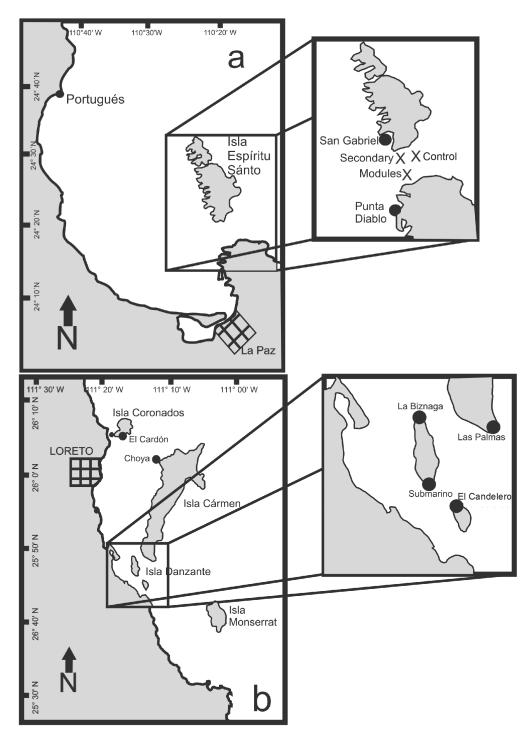


FIGURE 1. Study sites: (a) Bahía de La Paz; (b) Bahía de Loreto. X indicates ship grounding sites.

sites were at San Lorenzo reef. The first is a restored reef, consisting of 30 modules of concrete and rock on which fragments of Pocillopora spp. were cemented. This area (847 m²) was severely disturbed by the grounding of a tanker ship on 22 September 2001 (we refer to this area as Modules). An area adjacent to Modules, of 7,625 m² (referred to as Secondary), was affected by coral fragments dispersed by Hurricane "Juliette" (Balart 2001). A third sampling site at San Lorenzo reef was a control area that was not affected by the tanker ship (referred to as Control). In addition, two sites were selected along the mainland coast (Punta Diablo and Portugués) and one at Isla Espíritu Santo (San Gabriel). In Bahía de Loreto (Figure 1*b*), two sites were selected at Isla Danzante (Submarino and La Biznaga), one at an islet south of Isla Danzante (El Candelero), two at Isla Carmen (Choya and Las Palmas), and one at Isla Coronados (El Cardón).

Recruitment and Sea-Surface Temperature

To quantify the number of recruits, terracotta tiles (24 by 9.4 by 2.5 cm) were tied to the modules, rocks, and/or coral colonies using a synthetic rope, at depths of 1 to 5 m. Tiles were tied with some separation from the modules, rocks, or corals in such a way that the entire tile surface was accessible for recruitment. The total available settlement area of each tile was 0.062 m². To assess spatial variation in recruitment, 30 tiles were placed in the restored area, and six tiles were placed in the other study sites. The difference in the numbers of tiles was due to the priority of detecting recruits in the restored reef area. To estimate the temporal variation of recruitment at each site, all tiles were removed and replaced approximately every 3 months. The average exposure time of each tile was 95 days, and the total exposure time was 478 days in Bahía de La Paz (from June 2004 to September 2005) and 354 days in Bahía de Loreto (from August 2004 to July 2005). In total, 150 tiles were placed in the restored reef, and 24 tiles were placed in the remaining sites. Some tiles were lost in the study between sampling campaigns due to environmental action and therefore were not considered in the analysis (see Table 1).

Terracotta tiles were extracted from the sites and fixed in 4% formalin. Later, tiles were rinsed in a solution of 20% sodium hypochlorite for 24 hr to remove all organic matter (López-Pérez et al. 2007). A stereoscopic microscope (Olympus SZ40) was used to count and measure coral recruits on all tiles. Identification of recruits was made using available literature (Babcock et al. 2003, Minton and Lundgren 2006). Photographs of samples of *Psammocora*, *Porites*, *Pocillopora*, and *Tubastrea* recruits were taken with a scanning electron microscope (Hitachi S-3000N) to corroborate microscope identification.

Recruitment was calculated as density (ind m⁻²), dividing the number of recruits by the analyzed surface of each site, considering each terracotta tile as an individual sampling unit. Annual recruitment rate (ind m⁻² yr⁻¹) was calculated by multiplying the calculated density for each site for 365 days and dividing it by the total exposure time of each site (478 days in Bahía de La Paz and 354 days in Bahía de Loreto). To evaluate spatial (sites) and temporal (months) differences on recruitment, we applied a one-way analysis of variance (ANOVA); data were normalized previously by transformation $(\log x + 1)$ to approach normality. Post hoc comparison of means was performed using Tukey's HSD for unequal number of samples.

During the study period, in situ SST was recorded every hour in all locations using underwater thermograph data loggers (HOBO Pendant Temperature, Onset Computer Corporation, Bourne, Massachusetts, U.S.A.) at 3 m depth. Linear regressions were used to assess relationships between coral recruitment and average temperature of each sampled period.

RESULTS

Spatial Analysis

A total of 115 coral recruits was recorded: 110 were recruited at Bahía de La Paz and five at Bahía de Loreto. Five coral genera were identified among recruits at Bahía de La Paz

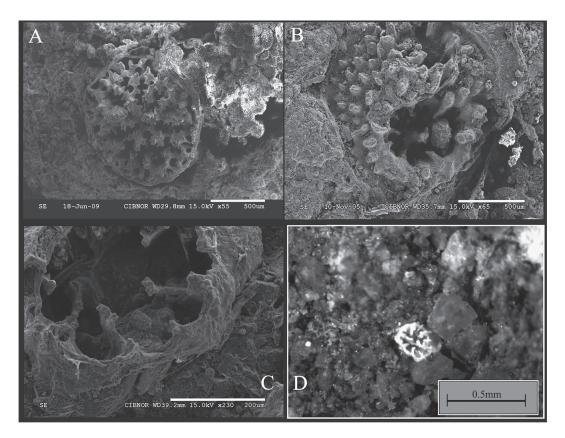


FIGURE 2. Photographs of recruits: (A) Porites, scanning electron microscope, 55×; (B) Pocillopora, scanning electron microscope, 65×; (C) Tubastrea, scanning electron microscope, 230×; (D) Pavona, stereoscopic microscope, 4×.

(Figure 2, Figure 3); *Porites* was the dominant genus (99 recruits, 6.54 ind m⁻²), followed by *Pocillopora* (six, 0.39 ind m⁻²), *Psammocora* (three, 0.19 ind m⁻²), and *Pavona* and *Tubastraea* (one each, 0.06 ind m⁻²). At Bahía de Loreto, two coral genera were recorded, *Porites* (four, 0.77 ind m⁻²) and *Psammocora* (one, 0.19 ind m⁻²).

Average recruit density at Bahía de La Paz was 16.76 ± 38.74 ind m⁻². The recruitment maximum was found in Punta Diablo (95 recruits, 95.77 ind m⁻²), and the minimum was found in Portugués (0.90 ind m⁻²). Modules, San Gabriel, and Portugués had 11, three, and one recruits, respectively; no recruits were found at Secondary and Control sites. All the *Pocillopora* recruits (n = 6) were found at Modules (Table 1). All sites were statistically similar except for Punta Diablo (F = 2.57; df = 5, 29; P < .05).

In Bahía de Loreto, three *Porites* recruits were found at Submarino (3.84 ind m⁻²), one *Porites* (1.19 ind m⁻²) in El Candelero, and one *Psammocora* (0.92 ind m⁻²) in Las Palmas. No recruits were found at Choya, El Cardón, or La Biznaga (Table 2). No differences were found among sites (F = 1.19; df = 5, 23; P > .05).

Temporal Analysis

Higher coral recruitment (F = 2.08; df = 4, 29; P < .05) (Table 2) was recorded during warm seasons of 2004 (38.04 ± 86.75 ind m⁻²) and 2005 (7.53 ± 18.44 ind m⁻²) at Bahía de La Paz; recruitment pulses corresponded to

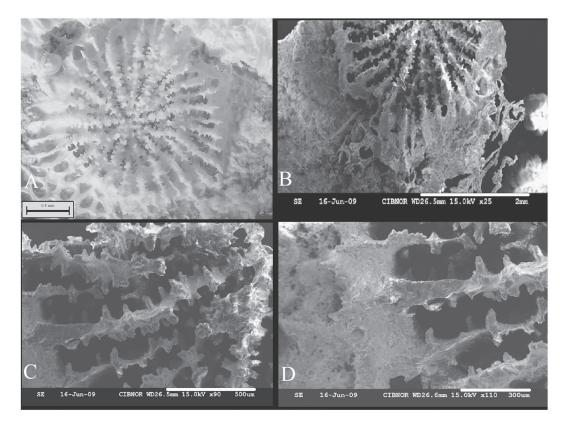


FIGURE 3. Photographs of *Psammocora* sp. recruit settled in this study: (A) stereoscopic microscope, $2\times$; (B) scanning electron microscope, $25\times$; (C) scanning electron microscope, $90\times$; (D) scanning electron microscope, $110\times$.

TABLE 1

Number of Analyzed Terracotta Tiles, Analyzed Area, Recruits, Recruit Density, and Annual Recruitment Rate						
by Location in Bahía de La Paz and Bahía de Loreto						

Bahía	Study Sites	Recovered Settlement Plates	Analyzed Area (m ²)	Recruits (ind)	Recruit Density (ind m ⁻²)	Annual Recruitment Rate (ind m ⁻² yr ⁻¹)
La Paz	Modules	146	9.05	11	1.22	0.93
	Secondary	23	1.43	0	0	0
	Control	23	1.43	0	0	0
	Punta Diablo*	16	0.99	95	95.77	73.13
	San Gabriel	18	1.12	3	2.69	2.05
	Portugués	18	1.12	1	0.90	0.68
	Average \pm SD	40.67 ± 51.68	2.52 ± 3.20	18.33 ± 37.79	16.76 ± 38.72	12.80 ± 29.57
Loreto	Las Palmas	18	1.12	1	0.90	0.92
	Choya	17	1.05	0	0	0
	Submarino	13	0.81	3	3.72	3.84
	El Cardón	9	0.56	0	0	0
	La Biznaga	12	0.74	0	0	0
	El Candelero	14	0.87	1	1.15	1.19
	Average \pm SD	13.83 ± 3.31	0.86 ± 0.21	0.83 ± 1.17	0.96 ± 1.44	0.99 ± 1.49

* Significant differences between sites at P < .05.

		В	ahía de La Paz			
Site	Jun.–Aug. 2004	Aug.–Nov. 2004*	Nov.–Feb. 2005	Feb.–Jun. 2005	Jun.–Sept. 2005	Average ± SD
San Lorenzo	1.61	3.76	0.54	0	0	1.18 ± 1.58
Punta Diablo*	0	215.05	0	3.23	45.16	52.69 ± 92.76
San Gabriel	0	5.38	0	2.30	0	1.54 ± 2.37
Portugués	0	4.03	0	0	0	0.81 ± 1.80
Average \pm SD	0.40 ± 0.81	57.06 ± 105.33	0.14 ± 0.27	1.38 ± 1.64	11.29 ± 22.58	
		В	ahía de Loreto			
Site	Aug.–Oct. Oct.–J 2004 2005			an.–Apr. 2005	Apr.–Jul. 2005	Average ± SD
Submarino	0	1.40)	0.62	0	0.51 ± 0.66
El Candelero	1.47	0		0	0	0.37 ± 0.74
as Palmas 0		1.00	0	0	0	0.25 ± 0.50
Average \pm SD	0.49 ± 0.12	85 0.80 ±	$0.72 0.21 \pm 0.36$		0 ± 0	

 $\label{eq:TABLE 2} TABLE \ 2$ Density of Recruits (ind m^2) at Each Site in Bahía de La Paz and Bahía de Loreto by Time Period

Note: No recruits were found in Secondary, Control, Choya, El Cardón, and La Biznaga, so these sites are not included in the table. * Significant differences between time periods at P < .05.

maximum SST records (~28°C) (Figure 3). Minimum recruit density (0.09 ± 0.22 ind m⁻²) was found from November 2004 to February 2005, coinciding with the lowest SST record (~21°C).

The average annual recruitment rate at Bahía de La Paz was 12.80 ± 29.57 ind m⁻² yr⁻¹. Most recruits were found at Punta Diablo, with two periods of high recruitment: the first during August to November 2004 (77 *Porites* recruits and three *Psammocora* recruits) and another from June to September 2005 (14 *Porites* recruits) (Figure 4). Eleven coral recruits (six *Pocillopora*, three *Porites*, one *Tubastraea*, one *Pavona*) were observed at Modules from June of 2004 to February of 2005 (Figure 4, Table 2).

The average annual recruitment in Bahía de Loreto was 0.99 ± 1.49 ind m⁻² yr⁻¹; the highest density of recruits settled during the warm season of 2004 (August–October, 0.2 ± 0.6 ind m⁻²) and during winter (October 2004–January 2005, 0.35 ± 0.59 ind m⁻²) (Figure 4). No recruits settled during the warm season of 2005 (Figure 4). The warm season of 2004 corresponded to the maximum SST at Bahía de Loreto (~27°C). However, there were no significant differences in the number of recruits settled between the analyzed time periods (F = 0.69; df = 3, 23; P > .05). Linear regressions between the density of recruits and SST showed no significant association ($r^2 = 0.43$, N = 9, P > .05).

DISCUSSION

This is the first quantitative report of coral larval recruitment in the Gulf of California and the second highest record of coral recruits in the eastern Pacific [López-Pérez et al. (2007) registered 20.4 ind m^{-2} in Huatulco, Mexico]. Although most coral communities in the eastern Pacific are dominated by Pocillopora corals (Glynn and Ault 2000, Reves-Bonilla 2003), most of the coral recruits recorded in this study were Porites. This is in accordance with previous recruitment studies in the Pacific coast of Mexico, which showed *Porites* as a common coral recruit compared to other genera (Medina-Rosas et al. 2005, López-Pérez et al. 2007). This may be associated with the reproductive strategy of each species. Some authors (Stimson 1978, Harrison and Wallace 1990) mentioned that larvae produced by brooding species are larger and have more settlement success and higher

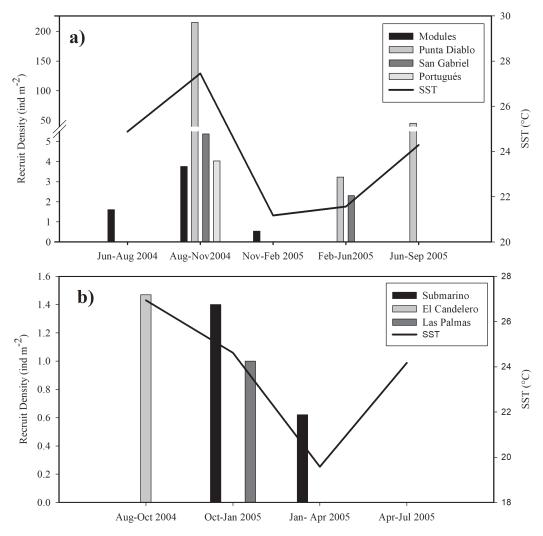


FIGURE 4. Density of coral recruits and sea-surface temperature (SST) per site and study period: (*a*) Bahía de La Paz; (*b*) Bahía de Loreto.

postfixation survival but have a shorter swimming phase compared to larvae derived from broadcast-spawner corals. In the eastern Pacific, *Porites* corals are known to be gonochoric brooders, and *Pocillopora* and *Pavona* are sequential hermaphroditic spawners (Glynn et al. 1991, Glynn et al. 1994, Glynn et al. 1996, Chávez-Romo and Reyes-Bonilla 2007, Rodríguez-Troncoso et al. 2011, Santiago-Valentín et al. 2015). There have been no previous reproductive studies in Mexico or the eastern Pacific of *Psammocora* corals. This is the first record of a *Psammocora* sexual recruit in the eastern Pacific (Figure 3); however studies in the Indo-Pacific show that they are gonochoric spawners (Baird et al. 2009). Successful recruitment of *Porites* found in our study could be associated with their brooding-type larvae. *Porites panamensis* is a known gonochoric coral that broods larvae throughout the year (Glynn et al. 1996, Rodríguez-Troncoso et al. 2011). Pocillopo-

rid corals can show sexual or asexual reproduction depending on local environmental conditions (Aranceta-Garza et al. 2012, Pinzón et al. 2012, Chávez-Romo et al. 2013). In our study, *Pocillopora* recruits were found in the restored area, confirming successful sexual recruitment derived from broadcast gametes in the area, as suggested by Chávez-Romo and Reyes-Bonilla (2007).

The recruitment rate found in this study is lower than that reported in the Caribbean (8.0 to 79 ind m^{-2} yr⁻¹), the Red Sea, and Indo-Pacific regions (over 100 ind $m^{-2} yr^{-1}$) (Table 3). These contrasting values may result from differences in species richness, coral cover, colony abundance, and oceanographic conditions in each region (Spalding et al. 2001). Sexual reproduction of corals is driven by environmental factors such as temperature, light, and nutrients (Harrison and Wallace 1990, Glynn et al. 1991). The highest recruitment season recorded in our study occurred during the warm months (summer) in both areas (Figure 2). This coincides with histological reports in the study area showing that during periods of high SST, reproductive activity of coral increases (Chávez-Romo and Reves-Bonilla 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011; Glynn, Colley, et al. 2017).

In the eastern Pacific, two regions, the Gulf of California (this study) and Oaxaca (López-Pérez et al. 2007), have shown higher recruitment rates (12.8 and 20.4 ind m⁻² yr⁻¹, respectively) in comparison with other eastern Pacific sites (less than 1.0 ind $m^{-2} yr^{-1}$: Birkeland 1977, Guzmán 1986, Glynn and Leyte-Morales 1997, Glynn et al. 2000, Medina-Rosas et al. 2005) (Table 3). Results of previous coral reproduction studies done along the Pacific coast of Mexico (Medina-Rosas et al. 2005, Chávez-Romo and Reves-Bonilla 2007, López-Pérez et al. 2007, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011; Paz-García, Chávez-Romo, et al. 2012) indicate that sexual reproduction has an important role in maintaining populations of coral in areas with high environmental seasonal variability. Studies conducted in Hawai'i and the Caribbean (Stimson 1978, Szmant 1986) showed that coral

under stressful environmental conditions and with high mortality rates tend to sexually reproduce several times through the year. However, Glynn et al. (1991), Glynn et al. (1994), Glynn et al. (1996), Glynn et al. (2000), and Glynn et al. (2011) found the opposite for many species of corals in Central America. Those authors stated that sexual reproduction is more common in optimal environments, and corals living in harsh environments often maintain their populations through asexual reproduction. The Pacific coast of Mexico has high environmental seasonal variability (temperature, tides, dissolved oxygen, nutrients, and organic matter) compared with southernmost regions of the eastern Pacific (Glynn and Ault 2000, Fiedler and Lavin 2017; Glynn, Alvarado, et al. 2017). Thus, our results agree with those of Stimson (1978) and Szmant (1986) and are opposed to what has been reported by Glynn et al. (1991), Glynn et al. (1994), Glynn et al. (1996), Glynn et al. (2000), and Glynn et al. (2011). Nevertheless, it may be a matter of spatial scale of each study because the works of Glynn et al. (1991), Glynn et al. (1994), Glynn et al. (1996), Glynn et al. (2000), and Glynn et al. (2011) were carried out in regions very close to each other with similar oceanographic conditions between sites, compared to the Pacific coast of Mexico, where documented sites are more distant from each other and the oceanographic conditions are more contrasting.

This study complements and confirms a coral recruitment trend reported by other authors in the eastern Pacific (Reves-Bonilla and Calderon-Aguilera 1994, Medina-Rosas et al. 2005, López-Pérez et al. 2007). This trend indicates higher recruitment rates in the northern region (Gulf of California) in comparison to lower-latitude localities (e.g., Jalisco, Oaxaca, and Central America); the only outlier site is Punta Diablo (Bahía de La Paz) where a very high recruitment rate was recorded. This may be attributed to particular oceanographic or structural conditions of that site. One possible hypothesis is that oceanic currents of Bahia de La Paz converge on Punta Diablo during some part of the year (Sánchez-Velasco et al. 2006, Obeso-Nieblas et al. 2007). Also, high productivity in the area

Site	$\begin{array}{c} \text{Recruitment} \\ \text{Rate (ind } m^{-2} \\ yr^{-1}) \end{array}$	Analyzed Area (m²)	Genus	Study
Eastern Pacific (Panamá)	1.06	1	2 Pocillopora	Birkeland (1977)
Eastern Pacific (Cabo Pulmo)	0.71	—	Porites	Reyes-Bonilla and Calderon- Aguilera (1994)
Eastern Pacific (Bahía Banderas)	1.08	16.76	9 Porites	Medina-Rosas et al. (2005)
Eastern Pacific (Bahías de Huatulco)	0.85-20.4	7.15	1 Pocillopora, 291 Porites	López-Pérez et al. (2007)
Eastern Pacific (Modules)	0.93	9.05	3 Porites, 6 Pocillopora, 1 Pavona, 1 Tubastraea	This study
Eastern Pacific (Punta Diablo)	73.13	0.99	92 Porites, 3 Psammocora	This study
Eastern Pacific (Portugués)	0.68	1.12	1 Porites	This study
Eastern Pacific (San Gabriel)	2.05	1.12	3 Porites	This study
Eastern Pacific (La Paz)	12.80 ± 29.57	2.52 ± 3.20	99 Porites, 6 Pocillopora, 3 Psammocora, 1 Pavona, 1 Tubastraea	This study
Eastern Pacific (Submarino)	3.84	0.81	3 Porites	This study
Eastern Pacific (El Candelero)	1.19	0.87	1 Porites	This study
Eastern Pacific (Las Palmas)	0.92	1.12	1 Psammocora	This study
Eastern Pacific (Loreto)	0.99 ± 1.49	0.86 ± 0.21	4 Porites, 1 Psammocora	This study
Indo-Pacific (Great Barrier Reef)	2092	40	NA	Sammarco et al. (1991)
Red Sea (Eliat)	190	10	680 Pocilloporidae, 150 Acroporidae	Glassom et al. (2004)
Caribbean (Colombia)	8.04	47	34 Agaricia, 34 Porites, 27 Montastrea, 24 Syderastrea, 21 Scolymia	Vidal et al. (2005)
Caribbean (Bermuda)	37	—	668 Porites, 13 Syderastrea, 1 Isophyllia	Smith (1992)
Caribbean (Barbados)	79	22.5	Agaricia, Porites, Pseudodiploria, Favia (90 recruits total, not specified by genus)	Hunte and Wittenberg (1992)

TABLE 3

Comparison of Coral Recruitment Studies Conducted in the Eastern Pacific, Indo-Pacific, Red Sea, and Caribbean, Showing Recruitment Rate and Coral Genus Reported in Each Study

Note: NA, not applicable.

has been reported (Reyes-Salinas et al. 2003, Verdugo-Díaz et al. 2014). These environmental conditions may, somehow, promote coral larval recruitment in the area, but this hypothesis deserves further scrutiny.

ACKNOWLEDGMENTS

We thank J. J. Ramirez-Rosas, M. Cota-Castro, and H. Bervera-León for their assistance in fieldwork; Ariel Cruz-Villacorta for the SEM operation and image acquisition of recruits; and N. Bocanegra Castillo for laboratory support, all of them from Centro de Investigaciones Biológicas del Noroeste (CIBNOR). We also thank A. Ortega Rubio and J. A. De Anda Montañez for support, and two anonymous reviewers whose recommendations substantially improved the manuscript.

Literature Cited

Aranceta-Garza, F., E. F. Balart, H. Reyes-Bonilla, and P. Cruz-Hernández. 2012. Effect of tropical storms on sexual and asexual reproduction in coral *Pocillopora verrucosa* subpopulations in the Gulf of California. Coral Reefs 31:1157–1167.

- Babcock, R. C., A. H. Baird, S. Piromvaragorn, D. P. Thompson, and B. L. Willis. 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool. Stud. 42:211–226.
- Baird, A. H., J. R. Guest, and B. L. Willis. 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu. Rev. Ecol. Evol. Syst. 40:531–571.
- Balart, E. F. 2001. Evaluación del impacto sobre fondos marinos coralinos producido por el encallamiento del Buque-Tanque Lázaro Cárdenas II, al sur de la isla Espíritu Santo, Baja California Sur. Informe Final para PROFEPA. Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur.
- Birkeland, C. 1977. The importance of biomass accumulation in early stages of benthic communities to the survival of coral reefs. Pages 15–21 *in* Vol. 1. Proc. 3rd Int. Coral Reef Symp., Miami.
- Carpizo-Ituarte, E., V. Vizcaíno-Ochoa, G. Chi-Barragán, O. Tapia-Vázquez, A. L. Cupul-Magaña, and P. Medina-Rosas. 2011. Evidence of sexual reproduction in the hermatypic corals *Pocillopora damicornis, Porites panamensis*, and *Pavona gigantea* in Banderas Bay, Mexican Pacific. Cienc. Mar. 37:97–112.
- Chávez-Romo, H. E., D. A. Paz-García, F. Correa-Sandoval, H. Reyes-Bonilla, R. A. López-Pérez, and P. Medina-Rosas. 2013.
 Difference in reproductive strategies of two scleractinian corals (branching vs massive) along the west coast of Mexico. Cienc. Mar. 39:387–400.
- Chávez-Romo, H. E., and H. Reyes-Bonilla. 2007. Reproducción sexual del coral *Pocillopora damicornis* al sur del Golfo de California, México. Cienc. Mar. 33:495– 501.
- Fiedler, P. C., and M. F. Lavin. 2017. Oceanographic conditions of the eastern tropical Pacific. Pages 59–83 in P. W. Glynn, D. P. Manzello, and I. C. Enochs, eds. Coral

reefs of the eastern tropical Pacific. Persistence and loss in a dynamic environment. Coral reefs of the world, vol. 8. Springer, Dordrecht.

- Fox, H. E. 2004 Coral recruitment in blasted and unblasted sites in Indonesia: Assessing rehabilitation potential. Mar. Ecol. Prog. Ser. 269:131–139.
- Glassom, D., D. Zakai, and N. E. Chadwick-Furman. 2004. Coral recruitment: A spatio-temporal analysis along the coastline of Eliat, Northern Red Sea. Mar. Biol. (Berl.) 144:641–651.
- Glynn, P. W., J. J. Alvarado, S. Banks, J. Cortés, J. S. Feingold, C. Jiménez, J. E. Maragos, P. Martínez, J. L. Maté, D. A. Moanga, S. Navarrete, H. Reyes-Bonilla, B. Riegl, F. Rivera, B. Vargas-Angel, E. A. Wieters, and F. A. Zapata. 2017. Eastern Pacific coral reef provinces, coral community structure and composition: an overview. Pages 107–176 *in* P. W. Glynn, D. P. Manzello, and I. C. Enochs, eds. Coral reefs of the eastern tropical Pacific. Persistence and loss in a dynamic environment. Coral reefs of the world, vol. 8. Springer, Dordrecht.
- Glynn, P. W., and J. S. Ault. 2000. A biogeographic analysis and review of the far eastern Pacific coral region. Coral Reefs 19:1–23.
- Glynn, P. W., S. B. Colley, E. Carpizo-Ituarte, and R. H. Richmond. 2017. Coral reproduction in the eastern Pacific. Pages 435–476 in P. W. Glynn, D. P. Manzello, and I. C. Enochs, eds. Coral reefs of the eastern tropical Pacific. Persistence and loss in a dynamic environment. Coral reefs of the world, vol. 8. Springer, Dordrecht.
- Glynn, P. W., S. B. Colley, C. M, Eakin, D. B. Smith, J. Cortes, N. J. Gassman, H. M. Guzman, J. B. Del Rosario, and J. S. Feingold. 1994. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). II. Poritidae. Mar. Biol. (Berl.) 118:191–208.
- Glynn, P. W., S. B. Colley, N. J. Gassman, K. J. Black, J. Cortes, and L. Math. 1996. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos

Islands (Ecuador). III. Agariciidae (*Pavona gigantea* and *Gardineroseris planulata*). Mar. Biol. (Berl.) 125:579–601.

- Glynn, P. W., S. B. Colley, H. M. Guzman, C. Enochs, J. Cortés, J. L. Maté, and J. S. Feingold. 2011. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and the Galápagos Islands (Ecuador). VI. Agariciidae, *Pavona clavus*. Mar. Biol. (Berl.) 158:1601–1617.
- Glynn, P. W., S. B. Colley, J. H. Ting, J. L. Maté, and H. M. Guzmán. 2000. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp. Mar. Biol. (Berl.) 36:785–805.
- Glynn, P. W., N. J. Gassman, C. M. Eakin, J. Cortes, D. B. Smith, and H. M. Guzman. 1991. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador) I. Pocilloporidae. Mar. Biol. (Berl.) 109:355–368.
- Glynn, P. W., and G. E. Leyte-Morales. 1997. Coral reefs of Huatulco, West México: Reef development in upwelling Gulf of Tehuantepec. Rev. Biol. Trop. 45:1033–1047.
- Guzmán, H. M. 1986. Estructura de la comunidad arrecifal en Isla Del Caño, Costa Rica, y el efecto de perturbaciones naturales severas. M.S. thesis, Universidad de Costa Rica.
- Harrison, P. C., and C. C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. Pages 133–207 *in* Z. Dubinsky, ed. Ecosystems of the world. Vol. 25. Coral reefs. Elsevier, Amsterdam.
- Heyward, J., and A. P. Negri. 2010. Plasticity of larval pre-competency in response to temperature: Observations on multiple broadcast spawning coral species. Coral Reefs 29:631–636.
- Hunte, W., and M. Wittenberg. 1992. Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. Mar. Biol. (Berl.) 114:625–631.
- López-Pérez, R. A., M. G. Mora-Pérez, and G. E. Leyte-Morales. 2007. Coral (Anthozoa: Scleractinia) recruitment at Bahías de

Huatulco, western México: Implications for coral community structure and dynamics. Pac. Sci. 61:355–369.

- Manzello, D. P., J. A. Kleypas, D. A Budd, C. M. Eakin, P. W. Glynn, and C. Langdon. 2008. Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO₂ world. Proc. Natl. Acad. Sci. U.S.A. 105:10450–10455.
- Medina-Rosas, P., J. D. Carriquiry, and A. L. Cupul-Magaña. 2005. Recruitment of *Porites* (Scleractinia) on artificial substrate in reefs affected by the 1997–98 El Niño in Banderas Bay, Mexican Pacific. Cienc. Mar. 31:1–7.
- Miller, K. J., and D. J. Ayre. 2004. The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. J. Hered. 92:557–568.
- Minton, D., I. Lundgren, and A. Pakenham. 2007. A two-year study of coral recruitment and sedimentation in Asan Bay, Guam. Unpubl. report, National Park Service, War in the Pacific National Historical Park, Hagatna, Guam.
- Obeso-Nieblas, M., B. Shirasago-German, J. H. Gavino-Rodríguez, H. Obeso-Huerta, E. L. Pérez-Lezama, and A. R. Jiménez-Illescas. 2007. Hydrography at the North Mouth of La Paz Bay, Baja California Sur, Mexico. Cienc. Mar. 33:281–291.
- Paz-García, D. A., E. F. Balart, and F. J. García-de-Léon. 2012. Cold water bleaching of *Pocillopora* in the Gulf of California. Pages 9–10 *in* Proc. 12th Int. Coral Reef Symp., Cairns.
- Paz-García, D. A., H. E. Chávez-Romo, F. Correa-Sandoval, H. Reyes-Bonilla, A. López-Pérez, P. Medina-Rosas, and M. P. Hernández-Cortés. 2012. Genetic connectivity patterns of corals *Pocillopora damicornis* and *Porites panamensis* (Anthozoa: Scleractinia) along the west coast of Mexico. Pac. Sci. 66:43–61.
- Pinzón, J. H., H. Reyes-Bonilla, I. B. Baums, and T. C. LaJeunesse. 2012. Contrasting clonal structure among *Pocillopora* (Scleractinia) communities at two environmentally

distinct sites in the Gulf of California. Coral Reefs (doi:10.1007/s00338-012-0887-y).

- Reyes-Bonilla, H. 2003. Coral reefs of the Pacific coast of Mexico. Pages 331–349 *in* J. Cortés, ed. Latin American coral reefs. Elsevier Science, Amsterdam.
- Reyes-Bonilla, H., and L. E. Calderón-Aguilera. 1994. Parámetros poblacionales de *Porites Panamensis* (Anthozoa: Scleractinia) en el arrecife de Cabo Pulmo, México. Rev. Biol. Trop. 42:121–128.
- Reyes-Bonilla, H., J. D. Carriquiry, G. E. Leyte-Morales, and A. L Cupul-Magaña. 2002. Effects of the El Niño-Southern Oscillation and the anti–El Niño event (1997–1999) on coral reefs of the western coast of México. Coral Reefs 21:368– 372.
- Reyes-Salinas, A., R. Cervantes-Duarte, R. A. Morales-Pérez, and J. E. Valdez-Holguín. 2003. Variabilidad estacional de la productividad primaria y su relación con la estratificación vertical en la Bahía de La Paz, BCS. Hidrobiologica 13:103–110.
- Richmond, R. R. 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. Proc. 5th Int. Coral Reef Symp., Tahiti 6:101–106.
- Ritson-Williams, R., V. J. Paul, S. N. Arnold, and R. S. Steneck. 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. Coral Reefs 29:71–81.
- Rodríguez-Troncoso, A. P., E. Carpizo-Ituarte, G. E. Leyte-Morales, G. Chi-Barragán, and O. Tapia-Vázquez. 2011. Sexual reproduction of three coral species from the Mexican South Pacific. Mar. Biol. (Berl.) (doi:10.1007/s00227-011-1765-9).
- Sammarco, P. W., J. C. Andrews, and M. J. Risk. 1991. Coral reef geomorphology as a function of seasonal prevailing currents and larval dispersal. Palaeogeogr. Palaeoclimatol. Palaeoecol. 88:1–12.

Sánchez-Velasco, L., E. Beier, C. Avalos-

García, and M. F. Lavín. 2006. Larval fish assemblages and geostrophic circulation in Bahía de La Paz and the surrounding southwestern region of the Gulf of California. J. Plankton Res. 28:1081–1098.

- Santiago-Valentín, J. D., A. P. Rodríguez-Troncoso, E. Carpizo-Ituarte, F. Benítez-Villalobos, P. Torres-Hernández, and A. López-Pérez. 2015. Reproductive pattern of the reef-building coral *Pavona gigantea* (Scleractinia: Agariciidae) in southern Mexican Pacific. Cienc. Mar. 41:233–246.
- Smith, L. C., and T. P. Hughes. 1999. An experimental assessment of survival, reattachment and fecundity of coral fragments. J. Exp. Mar. Biol. Ecol. 235:147–164.
- Smith, S. R. 1992. Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: Comparisons to Caribbean and Pacific reefs. Am. Zool. 32:663– 673.
- Spalding, M. D., C. Ravilious, and E. P. Green. 2001. World atlas of coral reefs. WCMC-UNEP. University of California Press, Berkeley.
- Stimson, J. S. 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. Mar. Biol. (Berl.) 48:173–184.
- Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–54.
- Verdugo-Díaz, G., A. Martínez-López, M. M. Villegas-Aguilera, and G. Gaxiola-Castro. 2014. Producción primaria y eficiencia fotosintética en Cuenca Alfonso, Bahía de La Paz, Golfo de California, México. Rev. Biol. Mar. Oceanogr. 49:527–536.
- Vidal, A. M., C. M. Villami, and A. Acosta. 2005. Composición y densidad de corales juveniles en dos arrecifes profundos de San Andrés Isla, Caribe Colombiano. Bol. Invest. Mar. Cost. 34:211–225.
- Wellington, G. M. 1982. Depth zonation of corals in the Gulf of Panama: Control and facilitation by resident reef fishes. Ecol. Monogr. 52:223–241.